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THE FOSSIL RECORD OF AMPHIUMID SALAMANDERS[1]

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ABSTRACT. The first pre-Pleistocene records of amphiumid salamanders are described here. *Proamphiuma cretacea,* n. gen., n. sp., from the late Cretaceous Hell Creek Formation of Montana, differs from *Amphiuma* in having less well-developed vertebral muscle crests, basapophyses, and neural spines. The species is represented only by vertebrae. *Amphiuma jepseni,* n. sp., from the late Paleocene Polecat Bench Formation, Wyoming, is the earliest record of the modern genus. Its vertebrae do not differ from those of Recent *Amphiuma,* but its skull lacks the facial elongation characteristic of the modern species. It is represented by vertebrae and by a partial skull.

Widespread transgressive seas of the Cretaceous, by providing extensive coastal plains and abundant shallow-water riparian habitat, may have been a major factor in the evolution of amphiumids and other elongated, aquatic salamanders.

INTRODUCTION

No previous fossil record for the salamander family Amphiumidae has been described, except for two Pleistocene records, one reliable, the other spurious. Auffenberg and Goin (1959) and Brattstrom (1953) have correctly ascribed to *Amphiuma* specimens from Florida Pleistocene localities. An unusual zoogeographic record was described for the Pleistocene of Germany by Brunner (1956), as a new species, *Amphiuma norica.* This specimen may be the parasphenoid of a teleost; it bears no resemblance to that of *Amphiuma*, and there is no basis for the identification (Fig. 3g-h).

Study of a North American Cretaceous floodplain herpetofauna (Estes, 1964) has disclosed ancestors of some lower vertebrates now living only on the Gulf Coastal Plain of North America. The

[1] Fossil vertebrates from the late Cretaceous Hell Creek Formation, Montana: Contribution No. 3.

fauna of the latter region today differs in many ways from the ancient floodplain fauna, but both share the presence of the fishes *Amia*, *Lepisosteus*, *Acipenser*, a polyodontid, sirenid salamanders, crocodiles, the turtle *Trionyx*, and alligators. These animals today are all relicts of forms once widely distributed on floodplains of late Cretaceous epicontinental seas, the relict drainage of which is the Mississippi River system. The description here of another Gulf Coast element in the fossil fauna of the late Cretaceous of Montana and Paleocene of Wyoming is further indication of the relict nature and former wide distribution of the Gulf Coast forms noted above.

ACKNOWLEDGMENTS

I am grateful to Dr. Francis Rose for helpful suggestions. Dr. Glenn Jepsen has provided the Silver Coulee specimens, which are described here in advance of a collaborative paper on Silver Coulee lower vertebrates, and I take pleasure in naming the new species for him. Collection of the Princeton material was supported by the Scott Fund, Princeton University. This research has been supported in part by National Science Foundation Grant GB-7176. The figures are by Mr. Laszlo Meszoly.

FAMILY AMPHIUMIDAE

Proamphiuma cretacea, n. gen., n. sp.

(Figs. 1, 2)

Holotype. MCZ 3504, vertebra.

Paratypes. MCZ 3506-3509, 3627-3636, vertebrae; 3505, 3637, atlantes.

Locality. Bug Creek Anthills (BCA), 80 feet below the Tullock Formation in the west half of Section 9, T 22 N, R 43 E, McCone County, Montana; collected by A. D. Lewis and party.

Horizon. Hell Creek Formation.

Age. Late Cretaceous.

Diagnosis. An amphiumid with neural arch of atlas horizontal rather than dorsally-pointing posteriorly; vertebrae relatively narrower, more constricted medially, and with muscle crests, basapophyses, and neural spines less prominent than in Recent *Amphiuma* of comparable size; shares with *Amphiuma* described below the relatively more constricted centrum and neural arch.

Description. Centra amphicoelous, cotyles teardrop-shaped with thin internal coating of calcified cartilage; subcentral keel prominent or low, with or without channels for the segmental blood

vessels; prominent or flattened anterior basapophyses usually projecting beyond anterior centrum margin; indications of two closely-appressed rib-bearers appearing on the four anterior vertebrae, the

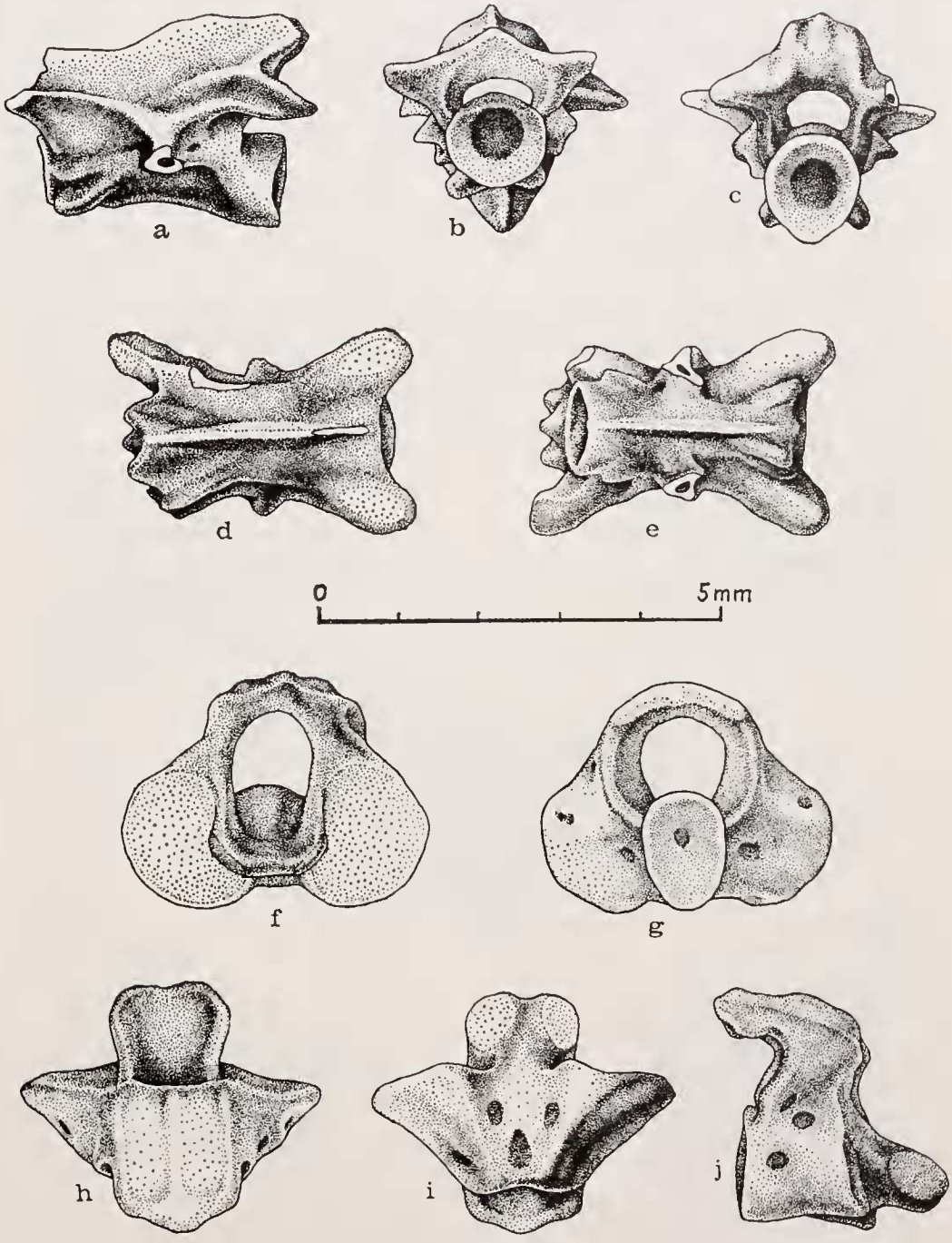

FIG. 1. *Proamphiuma cretacea*, n. gen., n. sp.: *a*, left lateral, *b*, anterior, *c*, posterior, *d*, dorsal, and *e*, ventral views of holotype vertebra, MCZ 3504; *f*, anterior, *g*, posterior, *h*, dorsal, *i*, ventral, and *j*, right lateral views of atlas, MCZ 3505.

others with only one; ventral lamina of rib-bearer present but apparently not well developed anteriorly; zygapophyses anteroposteriorly elongate, prominent, widely separated; posterior zygapophyses with keeled crests dorsally, extending forward to level of root of transverse process, these crests more medial in presumed anterior vertebrae and more lateral in presumed posterior vertebrae; neural spine relatively low, but prominent, thin and keeled, squared-off in lateral view; posterior border of spine slightly forked, often in three-pronged fashion. Atlantes with rounded anterior cotyles and prominent intercotylar process; centrum short; neural arch relatively high and blunt, with dorsal surface horizontal; neural spine only a faint ridge.

Discussion. The vertebrae are distinctively amphiumid in the combination of anterior basapophyses, subcentral keel, and posterior zygapophyses with prominent distinctive crests on their dorsal

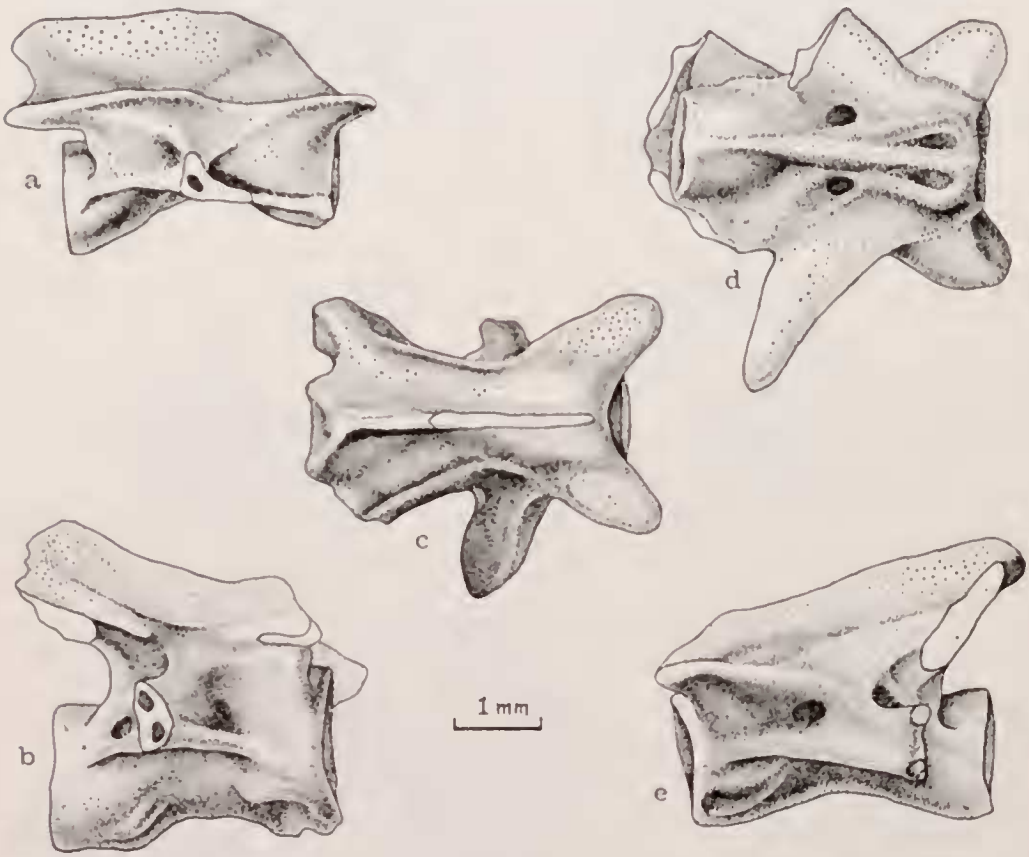

FIG. 2. *Proamphiuma cretacea*, n. gen., n. sp.: *a*, MCZ 3507, right lateral view of trunk vertebra; *b*, MCZ 3508, right lateral view of anterior trunk vertebra; *c*, MCZ 3506, dorsal view of trunk vertebra; *d* and *e*, MCZ 3509 — *d*, ventral, and *e*, left lateral views of trunk vertebra, probably near anterior end of column. White = broken surfaces.

surfaces that reach anteriorly to the roots of the transverse processes. There is close resemblance to vertebrae of *Amphiuma,* but specimens of equal size of the latter and of *Proamphiuma* differ in that the Cretaceous species has relatively narrower centra, less prominent zygapophyses, and weaker muscle crests. These are small differences but are on the order of those in closely-related modern salamander genera. Presence of posterior zygapophyseal crests implies development of the specialized IV-6 intervertebral muscle fibers found in Recent *Amphiuma* (Auffenberg, 1959).

No skull parts are known for this species, but the Paleocene *Amphiuma* described below has a less elongated snout than Recent *Amphiuma,* and probably a similar short skull was present in *Proamphiuma* as well. The two genera are closely related; *Proamphiuma* is structurally an ancestor of *Amphiuma* and there is no impediment to considering it a real ancestor, as well. It resembles the Paleocene *Amphiuma* described below in having relatively narrow, constricted centra. This is the earliest record of the Amphiumidae.

Amphiuma jepseni, n. sp.
(Figs. 3-5)

Holotype. Princeton University (PU) 14666, at least fourteen associated but dislocated vertebrae in a single block of matrix; associated left quadrate and left dentary.

Paratypes. PU 14668, partial skull and associated mandibles.

Locality and collector. Silver Coulee Quarry, S21, T 57 N, R 100 W, Park Co., Wyoming; collected by G. L. Jepsen and party.

Horizon. Polecat Bench Formation, Silver Coulee beds.

Age. Late Paleocene (Tiffanian).

Etymology. Named for its collector, Dr. G. L. Jepsen, Princeton University.

Diagnosis. Vertebrae relatively narrow as in *Proamphiuma,* crests and basapophyses well developed as in modern *Amphiuma;* snout short and blunt in contrast to modern *Amphiuma;* vomers less larval, with fewer and relatively more pointed teeth than in modern *Amphiuma.*

Description. Vertebrae amphicoelous, cotyles suboval anteriorly, teardrop-shaped posteriorly; anterior basapophyses strong, ventrally flattened, crested on their posterior surfaces, subcentral keel well defined, subcentral foramina simple, elongate; rib-bearers of posterior vertebrae unicipital, blunt distally, no rib articulation facet; anterior vertebrae with bicipital but closely approximated

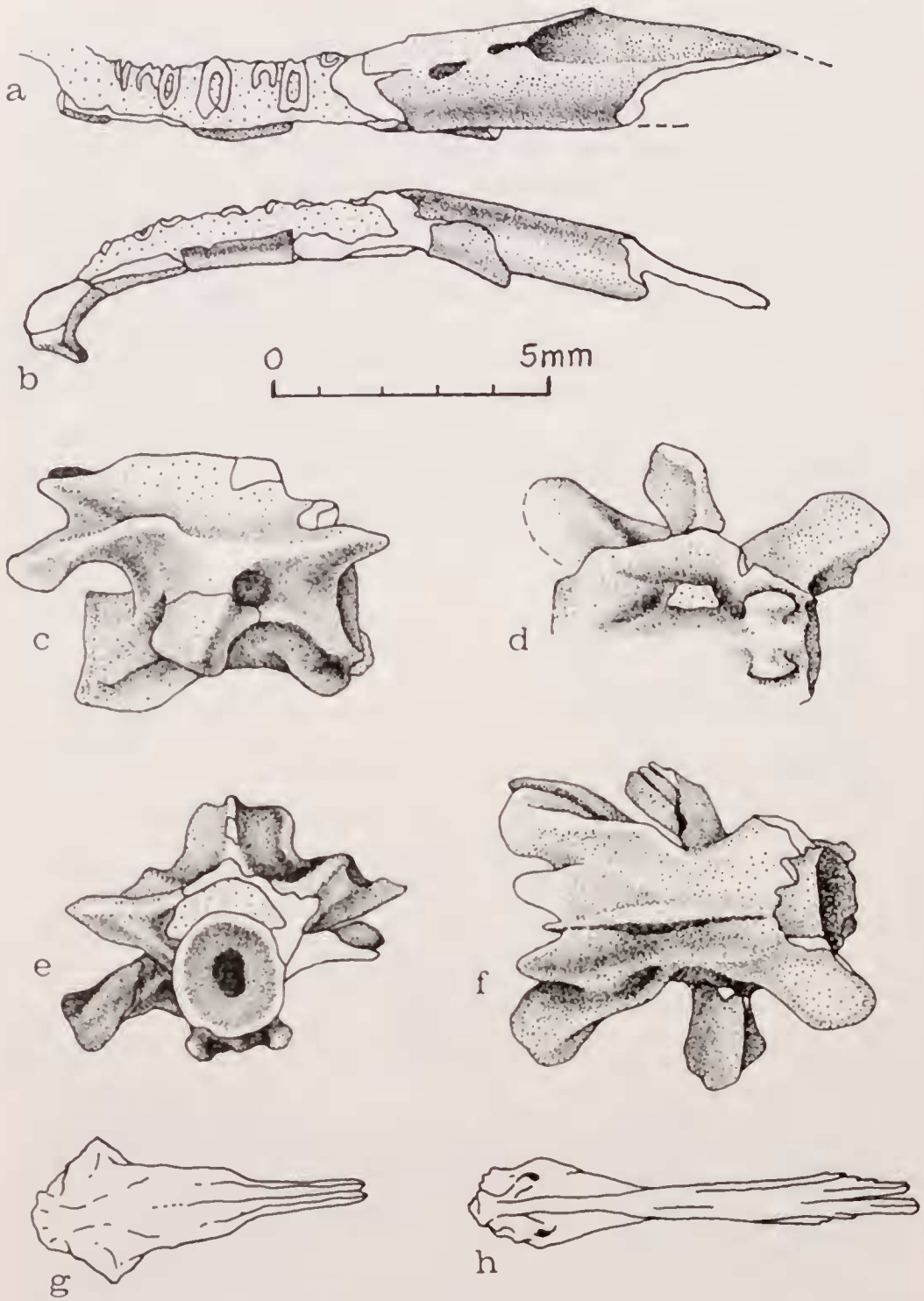

FIG. 3. *a - f*, *Amphiuma jepseni*, n. sp., PU 14666: *a*, labial, and *b*, ventral views of left dentary associated with holotype; *c*, right lateral, *d*, ventral, *e*, anterior, and *f*, dorsal views of best-preserved vertebra from holotype series. *g*, *A. means*, ventral view of parasphenoid; *h*, *A. norica* Brunner, ventral view of parasphenoid (?), after Brunner; *g*, *h*, × about 4. Coarse stipple = matrix, white area = broken surface.

rib-bearers; ventral lamina of transverse process prominent in posterior vertebrae, absent or reduced in anterior vertebrae; zygapophyseal ridge little developed near midpoint of vertebrae, neural arch narrow, pinched in at level of transverse process; well-developed keels on posterior zygapophyses reaching anteriorly to the level of transverse process; neural spine prominent, thin, squared off dorsally; posterior border of neural arch forked, a median septum bisecting the fork in three-pronged fashion.

Only anterior part of skull present, crushed and flattened, but restoration indicates a snout relatively wider and shorter than in *Amphiuma;* premaxilla unpaired, flattened dorsally, elongated posteriorly, a strong median septum formed, total actual tooth number not determinable because of breakage, but presence of a median tooth and six left lateral ones indicating a total of 13; ethmoid processes of frontals visible in section posteriorly; nasals not preserved, prefrontals sculptured, elongated, a long prefrontomaxillary

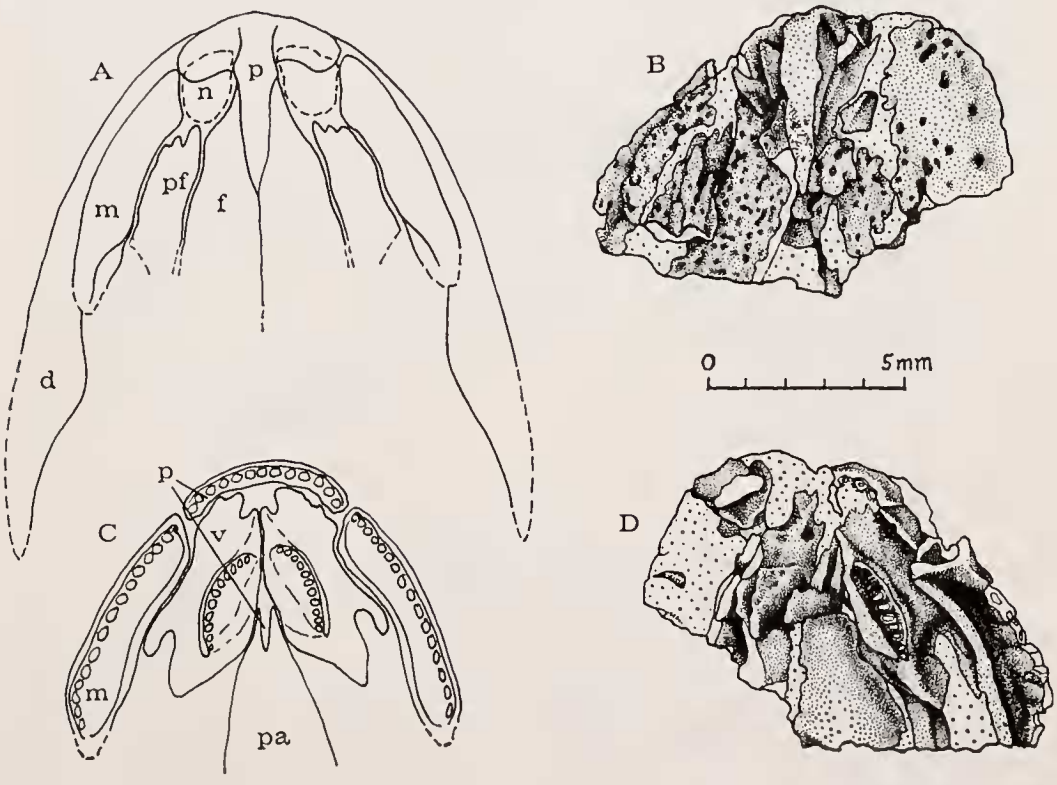

FIG. 4. *Amphiuma jepseni,* PU 14668, anterior portion of skull: A, restored dorsal view of snout and dentaries; B, dorsal view of fossil as preserved, right maxilla dislocated and flattened; C, restored palatal view; D, palatal view of fossil, elements of left side in approximately natural articulation. Abbreviations: d = dentary, f = frontal, m = maxilla, n = nasal, p = premaxilla, pa = parasphenoid, pf = prefrontal, v = vomer.

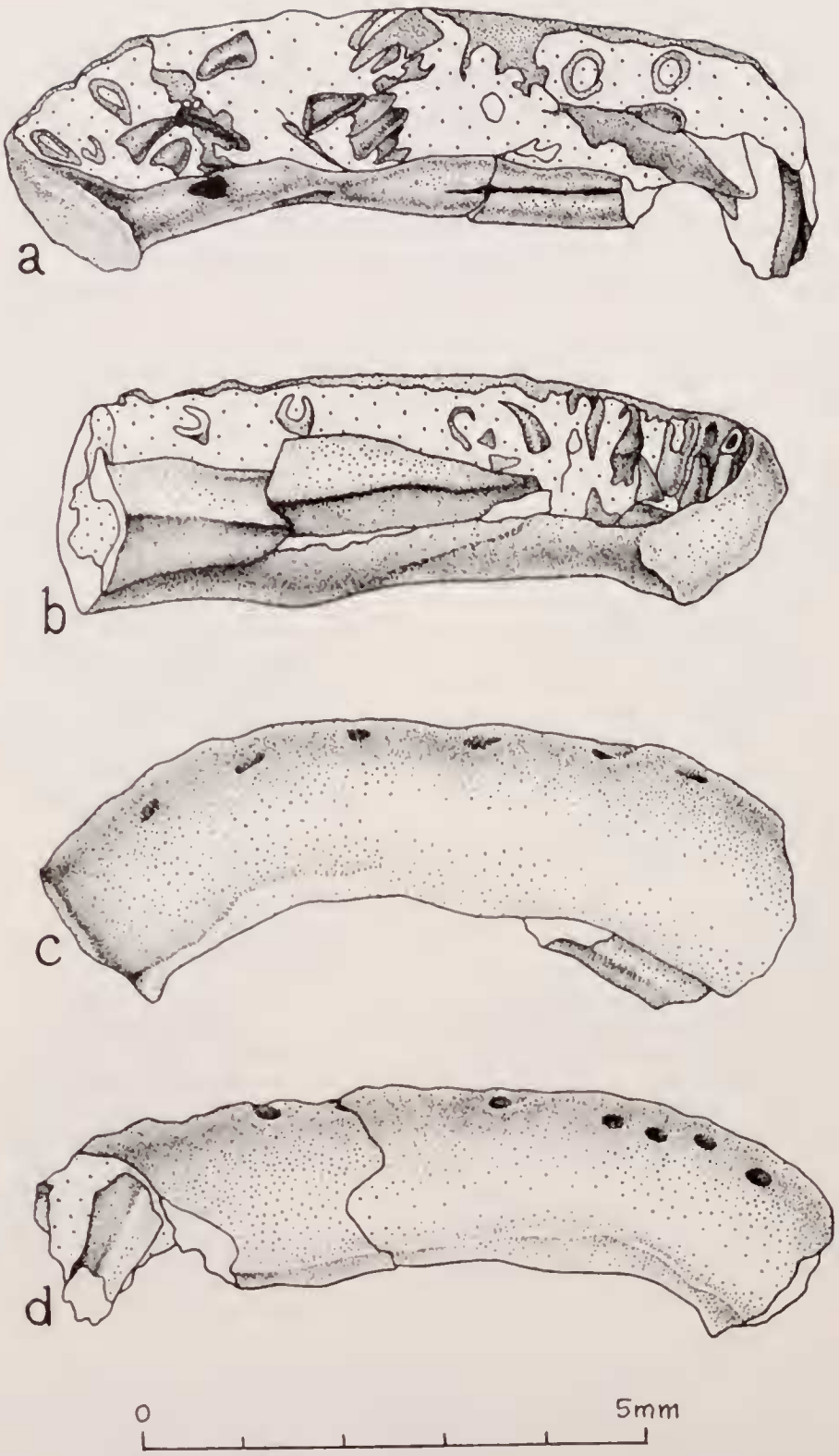

FIG. 5. *Amphiuma jepseni*, PU 14668, fragmentary dentaries originally in articulation with skull and removed to prepare palate: *a*, right lingual, *b*, left lingual, *c*, left ventral, and *d*, right ventral views.

suture extending posteriorly to orbit; frontal broken, dislocated, a strong sculpture present; maxilla bluntly curved, sculptured on nasal process, a row of foramina present exteriorly; teeth placed in a deep, channelled *sulcus dentalis;* teeth pedicellate, sharply pointed, and with recurved crowns, total tooth number unknown because of breakage; vomer expanded anteriorly, a small hollowed-out *sulcus dentalis* present near the midline, 10 or 11 teeth present, choanal excavation present laterally in vomer, reaching to level of seventh tooth from front; ethmoid visible medial to vomer, an anterior ethmoid foramen visible on the left; blunt parasphenoid extending anteriorly, covering ethmoids and separating vomers to anterior end of *sulcus dentalis;* orbitosphenoids missing, but grooves for them present on ventral surfaces of ethmoid; flange of vomer covers orbitosphenoid area ventrally.

Dentary strongly curved with deep *sulcus dentalis;* teeth as in upper jaw; symphysis flat, prominent; tooth number unknown, but comparison of dentary associated with type and PU 14668 indicates about 18; prearticular robust, medially crested, reaching anteriorly to about sixth tooth from symphysis; prominent fossa for adductor muscle attachment posterior to last tooth; blunt coronoid process present.

Quadrate blunt, robust, articular surface gently concave, palatoquadrate and hyoid connections well separated.

Discussion. Vertebrae of *Amphiuma jepseni* do not differ significantly from those of Recent species in general features, and are especially similar in degree of muscle crest development. Vertebrae of *Proamphiuma cretacea* have substantially less well-developed muscle crests relative to those of *A. jepseni* and Recent *Amphiuma* of equal size. The relatively constricted centra resemble those of *P. cretacea,* a resemblance not unlikely in view of their close geographic and temporal association.

The snout of *Amphiuma jepseni* is less elongated than that of Recent *Amphiuma,* although the specialized enclosure of olfactory tracts by the frontal is as well developed as in the Recent species. Tooth crowns of the fossil are less chisel-shaped than those of Recent species. Tooth number of premaxilla and dentary is within the range of Recent *Amphiuma,* but the number of vomerine teeth is significantly less (10-11 rather than 17-18; Rose, 1968). The latter condition and the greater development of vomers anterolateral to the tooth row indicate a lesser degree of paedomorphosis in *A. jepseni* than in Recent *Amphiuma.*

These skull differences probably reflect no more than specific difference from the Recent species. The lack of complete skeletons

of the fossil form and the existence of only two closely-related modern amphiumid species for comparison makes the differences somewhat difficult to assess. However, some substantiation of this conclusion can be drawn from the fact that *Proamphiuma cretacea* differs substantially in development of vertebral muscle crests when compared with *Amphiuma jepseni* and with Recent individuals of equal size. I consider these muscle crests to be useful in defining generic boundaries, since their development reflects muscle difference of greater adaptive significance to the animal than is elongation of the snout.

EVOLUTION AND FAUNAL ASSOCIATES

Other Cretaceous records of modern and extinct families of elongated, aquatic salamanders have also been described (Estes, 1964, 1969). The addition of amphiumid salamanders to this record suggests that the widespread epicontinental seas of the Cretaceous were an important factor in evolution of this abundant salamander fauna, by providing extensive coastal plains with slow drainage and abundant shallow-water, riparian habitats.

The presence of these amphiumids in Cretaceous (Maestrichtian) and Paleocene (Tiffanian) sediments in Wyoming and Montana implies an origin of the Amphiumidae earlier than the late Cretaceous. The family is thus almost equally as ancient as the Sirenidae, the earliest record of which occurs in rocks of late Cretaceous (Campanian) age in Wyoming (unpublished record of *Habrosaurus;* Estes, 1964, p. 170).

The reduction in size and numbers of dinosaurs and the presence of plant fossils of Paleocene aspect imply warm-temperate rather than sub-tropical conditions for the Bug Creek locality, which is stratigraphically close to the arbitrary Cretaceous-Paleocene boundary in Montana (Sloan and Van Valen, 1965).

The fauna at the Paleocene Silver Coulee locality is unusual for late Cretaceous and early Paleocene localities in that fish remains are lacking. However, the aquatic salamanders *Scapherpeton* and *Opisthotriton* occur at both Silver Coulee and Bug Creek localities.

LITERATURE CITED

AUFFENBERG, W.

1959. The epaxial musculature of *Siren*, *Amphiuma*, and *Necturus* (Amphibia). Bull. Florida State Mus. 4:253-265.

AUFFENBERG, W., AND C. GOIN
1959. The status of the salamander genera *Scapherpeton* and *Hemitrypus* of Cope. Amer. Mus. Novit. **1979**:1-12.

BRATTSTROM, B.
1953. Records of Pleistocene reptiles and amphibians from Florida. Journ. Florida Acad. Sci. **16**:243-248.

BRUNNER, G.
1956. Nachtrag zur Kleinen Teufelshöhle bei Pottstein (Ober-franken). Ein Übergang von der letzten interglaziale Riss-Würm-Warmfauna zur Würm I-Kaltfauna. Neues Jahrb. Geol. Pal., Monatsh., **1956**:75-100.

ESTES, R.
1964. Fossil vertebrates from the late Cretaceous Lance Formation, eastern Wyoming. Univ. Calif. Publ. Geol. Sci. **49**:1-180.
1969. The Batrachosauroididae and Scapherpetontidae, late Cretaceous and early Cenozoic salamanders. Copeia, 1969, no. 2, in press.

ROSE, F.
1968. Ontogenetic changes in the tooth number of *Amphiuma tridactylum*. Herpetologica, **24**:182-184.

SLOAN, R., AND L. VAN VALEN
1965. Cretaceous mammals from Montana. Science, **148**:220-227.

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